

Standing Waves in the Cochlea

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Abstract. Cochlear traveling waves are slow by two to three orders of magnitude compared to compressive wave propagation in the fluid. However, some observations are incongruent with the slow propagation. For instance, in the series of studies on cochlear wave propagation by Ruggero and his colleagues, the onset delay in cochlear mechanical response was inconsistent with the theory of slow traveling waves. The click response looked like the traveling wave initiates in the middle of the cochlea. In contrast, noise or pure tone response showed a gradual increase in onset delay from the base to the apex. An intriguing coincidence is that the cochlear coil has two distinct regions—a sound-port region in the base and a tubular region in the middle to apical locations. The sound-port region is a poor waveguide, unlike the tubular region. We investigated whether the standing waves in the mammalian cochlea can account for the observations by Ruggero and his colleagues. Using cochlear preparations excised from young gerbils, we compromised the cochlea waveguide to make it like a sound-port region. Under such conditions, we observed the co-existence of fast and slow traveling waves. Using computer models, we simulated three cochlear configurations: a fully tubular, a fully sound-port-like, and a hybrid model. Standing waves became more prominent in sound-port-like configuration, consistent with our excised cochlear experiments. Our results suggest that the current understanding of the spatiotemporal distribution of auditory signals has been over-simplified.

INTRODUCTION

Conventionally, the mammalian cochlea is represented by a long and narrow tube filled with fluid and separated by an elastic partition (Fig. 1A). Figure 2B is still a simplified representation of the cochlea but with two aspects more realistic anatomically. One is the location of two sound ports (e.g., the oval and round windows are not at the basal extreme). The other is the combination of the 3-D vestibule region in the base and the 1-D tubular region, based on scalar cross-sectional areas measured in rodent species (Fig. 1C). The anatomy suggests an acoustical segmentation in the cochlea. While the tubular region provides a proper waveguide, the 3-D sound-port region can favor near-instant pressure transmission from the oval window to a wide span of the cochlear epithelial coil. Interestingly, observations on the onset delay of cochlear traveling waves seemed consistent with this idea of anatomical segmentation (Temchin, Recio, 2012, Fig. 1D). Recio-Spinoso and Rhode (2015) suggested that fast compressive and slow traveling waves co-exist in the basal cochlea.

We tested the Recio-Spinoso-Rhode hypothesis by computationally and experimentally modifying the cochlear waveguide (the geometry of cochlear scalae). For computational simulations, we created three models: a conventional tube-like fluid space, a sound-port-like fluid space, and a realistic two-segment fluid space. For the

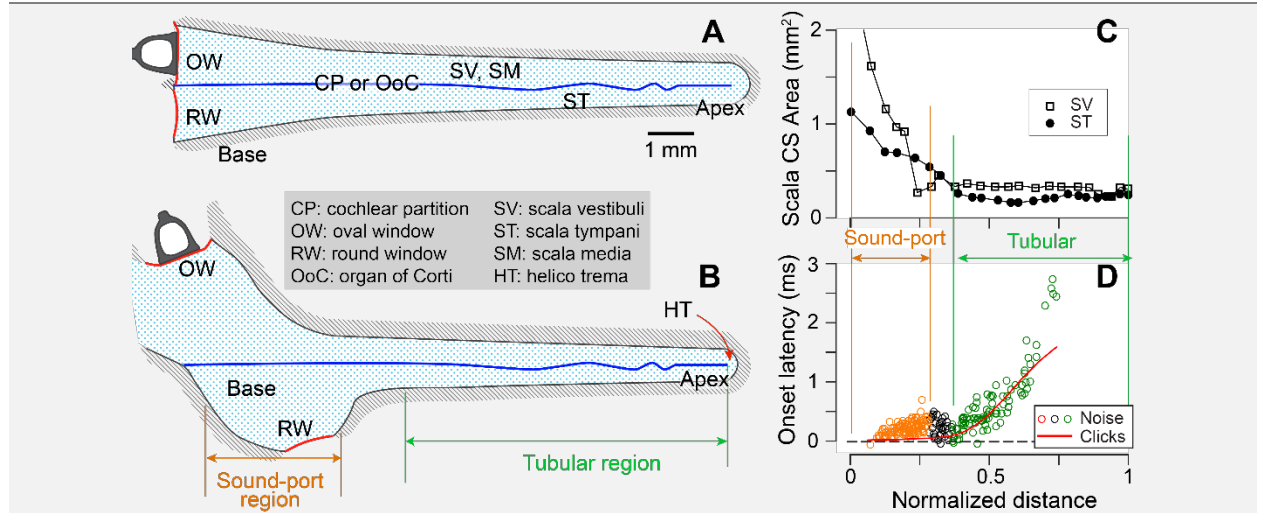


Figure 1. Anatomical and functional segments of the cochlea. The coiled cochlea is shown straightened for illustration. (A) The cochlear cavity is divided by the elastic cochlear partition (CP) into the scala vestibuli and scala tympani. The cochlea has two membrane-covered openings called the oval and the round windows (the sound-ports of OW and RW). (B) Cochlear models have simplified a geometric feature of the sound-port location, which could be relevant to hearing function. (C) The scala cross-sectional area along the cochlear length demonstrates the sound-port and the tubular regions. Data are from the chinchilla cochlea (Kim et al., 2008). (D) Experimental observations on the onset delay of cochlear traveling waves show two distinct zones along the cochlear length (Temchin et al., 2012). The two zones coincide with the anatomical sections.

experiment, we prepared two sets of excised cochlear preparations: one with wide openings above and below the cochlear partition and the other with a wide opening on the apical side.

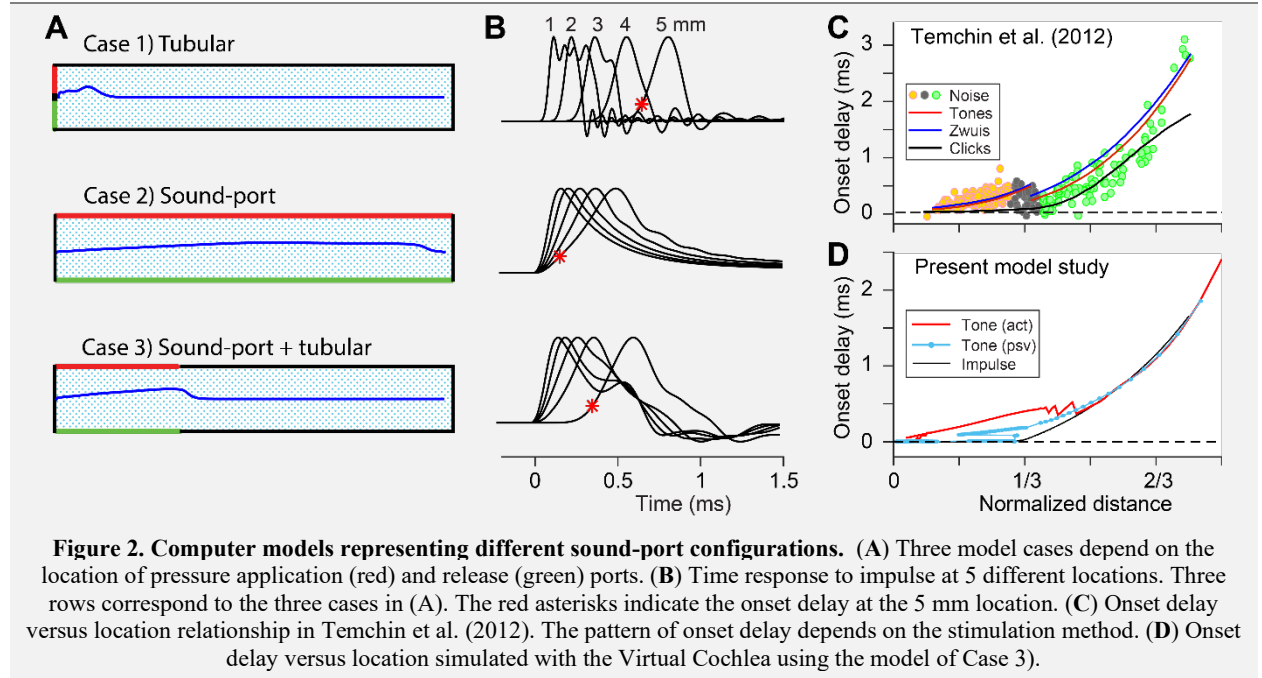
METHODS

Computational model: Virtual Cochlea

Our previous computational models (Liu, Gracewski et al. 2017; Prodanovic, Gracewski et al. 2019; Zhou and Nam 2019; Zhou, Jabeen et al. 2022) were modified for more realistic organ of Corti geometry acquired from our tomographic microscopy images (Jabeen et al., 2020; Zhou et al., 2022; Lin et al. 2024). The computer model incorporates structurally substantial organ of Corti components such as the inner and outer pillar cells, reticular lamina, hair cells, and Deiters cells, as well as its overlying tectorial membrane and underlying basilar membrane. Although our Virtual Cochlea is among the detailed cochlear models, it still simplified or neglected some potentially important details. For instance, three rows of outer hair cell-Deiters cell complex was lumped to one row; no explicit Corti fluid dynamics; no explicit sub-tectorial space fluid dynamics; straightened cochlear coil; 2-D scala fluid space; no nonlinearity. This study examined some realistic details relevant to the cochlear sound-port geometry that have been overlooked.

The cochlear fluid domain was represented as a 2-D rectangular box. The radial dimension of the cochlear fluid was reduced after approximating the radial vibrating pattern of the organ of Corti complex into a half-sine curve. Representing the gerbil cochlea, the box is 12.1 mm by 0.4 mm. The sound-port location was the primary testing parameter of this study (Fig. 2A). The control case at the top of Fig. 2A represents the conventional location of the sound-port—at the basal end. In one test case, the entire top boundary of fluid became a pressure inlet (the oval window) and the entire bottom boundary became a pressure release (the round window). The other test case represents the natural sound-port location of Fig. 1B. Although illustrated with a blue line in the middle of the fluid space, the partition in our computation model is a 3-D finite element model of the organ of Corti complex.

The computational model has about half a million degrees of freedom. It was solved in the time domain to simulate impulse responses and in the frequency domain to simulate the response to sinusoidal stimulations.



Experimental model: Sound-port-like preparation

Excised cochleae were prepared similarly to our previous studies (Zhou, Jabeen et al. 2022; Lin, Macić et al. 2024). Young Mongolian gerbils (15-30 days old, both sexes) were used for experiments according to the institutional guidelines of the University Committee on Animal Resources at the University of Rochester. The cochleae were acutely isolated and placed in a dissection dish filled with artificial perilymph (in mM 145 sodium gluconate, 7 NaCl, 3 KCl, 5 NaH_2PO_4 , 0.1 MgCl_2 , 5 D-glucose, 0.1 CaCl_2 , 5 HEPES; pH 7.3-7.4; 300 mOsm). Measurements were made at a target location: 6.5 or 8.5 mm from the basal end (Fig. 3A-D).

The cochlear bones were removed to expose the organ of Corti, and to examine different fluid boundary configurations. In one type of preparation (“Sound-port/Sound-port”, Fig. 3E), leaving only a single turn centered at the target location, the apical and basal turns were removed before being placed in the microchamber. The top and the bottom inter-scala bones were removed so that the exposed-mm-long cochlear coil was subjected to sound-port-like fluid pressures. In the other type of preparation (“Sound-port/Tube”, Fig. 3F), the apical turn of the target location was removed, but the basal turn was left intact. Only the top inter-scala bone was opened so that the top side was like the sound-port, but on the bottom side, the scala tympani was preserved.

A commercial optical coherence tomography system was used for vibration measurements (Ganymede, Thorlabs; center wavelength of 900 nm; A-scan rate 60 kHz; customized for 20x NA 0.4 objective). The vibrometry system was driven by a custom-written Matlab program. After scanning pseudo radial sections at multiple sites along the 0.8-1.2 mm-long cochlear coil, the longitudinal axis was defined along the root of the outer pillar cells. The longitudinal measurement section was along the first- or second-row outer hair cells. Over the open longitudinal span, 40-60 M-scans were acquired while multi-tone acoustic stimulation was delivered.

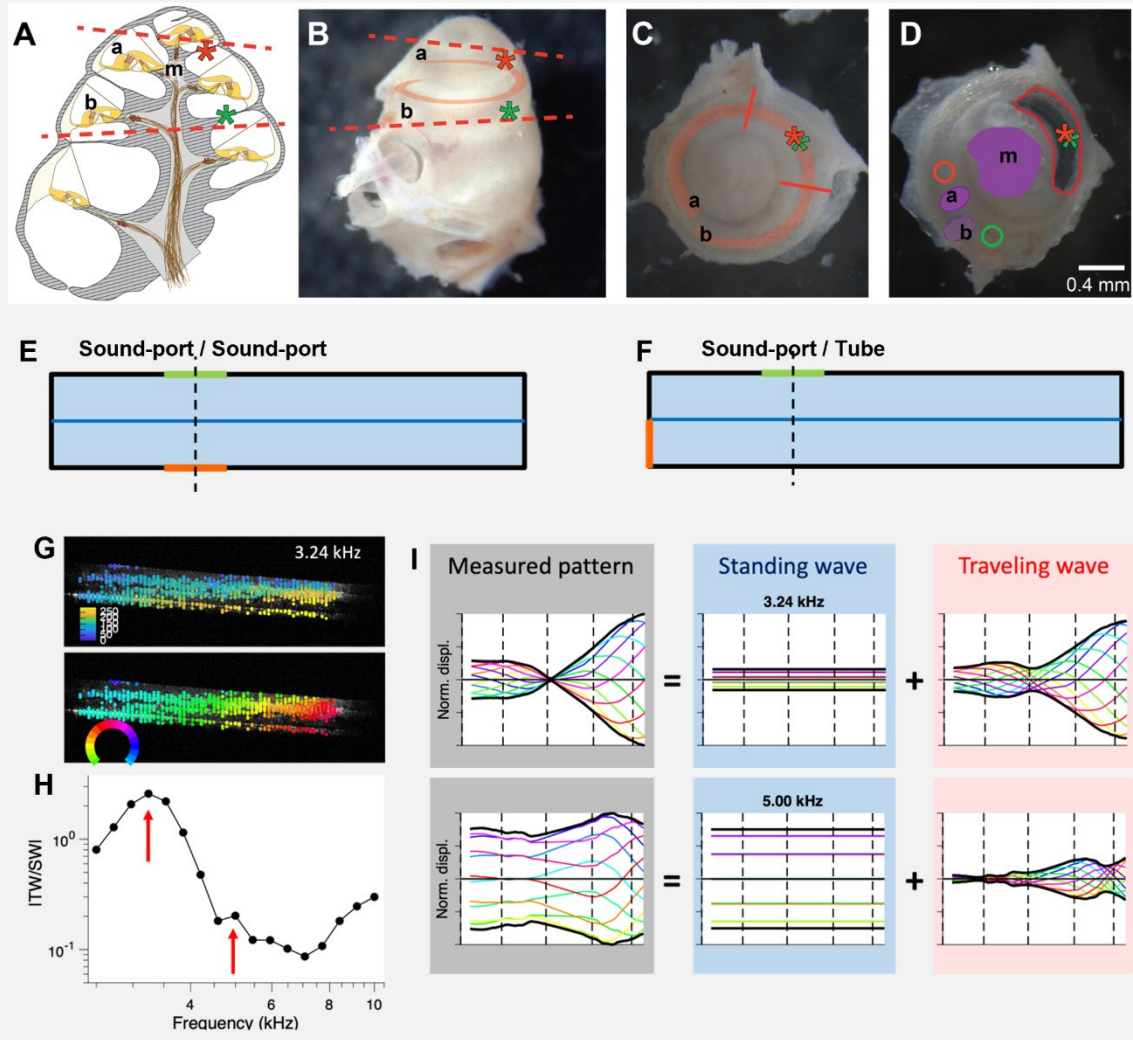


Figure 3. Excised cochlea with sound-port-like wide openings. (A, B) Vertical view of isolated cochlea. The broken lines indicate the place for circumferential cut. This example targeted 8.5 mm location from the basal end. The asterisks in (A) indicate the inter-scala bones to be removed. (C, D) Planar view of the cochlea before (C) and after (D) the removal of apical and basal turns. The pink coil indicates the remaining piece of epithelium after the cuts. The red lines (C, D) indicate the zone of exposure after the removal of the inter-scala bones. Cyanoacrylate glue (purple) applied at three places (m: modiolus, a: apical end, b: basal end). (E) The cochlea representing the preparation of (D) with wide openings of both top and bottom inter-scala bones. (F) Another preparation with only apical removal (basal turn intact). (G) Vibration of the cochlear coil along the longitudinal axis. The right-hand side is toward the apex. (H) The ratio of traveling wave to standing wave at different stimulating frequencies. (I) Spatial responses at the two frequencies (red arrows in panel (I)). The overall wave pattern was decomposed with a uniform displacement (named ‘Standing wave’) and a longitudinally varying displacement (‘Traveling wave’).

RESULTS

Co-existence of Fast and Slow Waves in Simulated Responses

Figure 2A shows the snapshot of cochlear partition deformation (blue curves) 0.1 ms after the impulse. For the ‘tubular’ case, the deformation occurred at the basal extreme next to the pressure source. Similarly, for the ‘sound-port + tubular’ case, the cochlear partition was deformed over the 4-mm span of the sound-port. For the ‘sound-port’ case, the entire cochlear span was agitated even at 0.1 ms after the impulse, suggesting the fast wave. Reflecting the stiffness gradient, the deformation increased toward the apex.

Figure 2B presents the displacement over time at five different locations ($x=1, 2, 3, 4$, and 5 mm from the base). The top plot faithfully illustrates the slow nature of the cochlear traveling wave. e.g., it took nearly 1 ms for the wave peak to arrive at the 5-mm location. It also shows the dispersive nature of the cochlear wave (monotonically increasing onset delay toward the apex).

Figure 2D shows the onset delay of the realistic ‘sound-port + tubular’ model versus the distance. Three curves represent the onset delay obtained from frequency responses of active (red) and passive (blue) cochlear models. The black curve is the onset delay obtained from the impulse response of the passive cochlea. As they should be, the onset delay values obtained from two stimulation protocols (pure tone and impulse) were comparable. Fig. 2C replicated Fig. 1D (Temchin et al. 2012) to facilitate comparison with our simulated result. Despite different species and approaches (chinchilla measurement versus gerbil simulations), the results compare well in several qualitative aspects. For instance, for the click, the little onset delay in the sound-port region is comparable to the impulse simulation results. The discontinuity in the onset delays due to sinusoidal stimulation, observed near the border between the two cochlear segments, was reproduced by the computer simulation. Our computer simulation predicted that if the cochlea is insensitive (say, suppressed or damaged outer hair cell motility), there would be little onset delay in the sound-port region.

Co-existence of Fast and Slow Waves in Measured Responses

It is impractical to modify the sound-port-like geometry of the natural cochlea into a tubular geometry. However, the other way was feasible—to modify the tubular region of the cochlea into a sound-port by creating wide openings (Fig. 3). Based on the simulated results in Fig. 2, we expected that the vibrations due to fast pressure transmission would become dominant and the cochlear traveling waves would largely disappear.

Figure 3A-D shows the procedures of our wide-opening (sound-port) preparation. Fig. 3E presents a cartoon version of the wide-opening preparation in a similar way to the models in Fig. 2. Acoustic pressures were expected to hit the exposed span of the cochlear coil (1.2 mm-long span enclosed with red curve) with little time difference ($< 1 \mu\text{s}$, based on the speed of the compressive wave in the water). As expected, we observed no sign of traveling waves: minimal phase difference along the length of the cochlear coil; 180 degrees phase drop across the best-responses frequency (Zhou et al. 2022).

We hypothesized that partial preservation of the tubular anatomy of the cochlea would preserve a fraction of traveling waves. To test that, unlike our standard preparation (Fig. 3D, E) with wide openings above and below the cochlear partition, the basal part of the cochlea was left intact while the apical turn from the place of observation was reduced. The resulting configuration is illustrated in Fig. 3F. In this preparation, the scala tympani still served as a waveguide while the scala media above the cochlear coil had a wide opening (0.8-1.2 mm).

Figure 3G shows the vibration pattern (amplitude and phase) along the exposed cochlear tissue (1 mm). The amplitude and phase varied along the cochlear length. The extent of longitudinal change of vibrations depended on the frequency (Fig. 3I). At 3.24 kHz, the slope of phase change was much greater than the vibrations at 5 kHz. We decomposed the overall response into two components: longitudinally uniform vibration (standing wave) and longitudinally varying vibration (traveling wave). The direction and extent of phase accumulation had the characteristics of cochlear traveling waves (phase decay toward the apex and more than 2π radians of change). The contribution of the traveling wave quickly dropped when the stimulating frequency was higher than 4 kHz. This also is consistent with the stalling characteristic of the cochlear traveling wave. That is, after the best frequency of a location, fast pressure waves prevailed.

CONCLUSIONS

Our results suggest that the cochlear basal region might respond differently from the rest of the cochlea because of its anatomy. While the 1-D tubular geometry of the cochlear scala serves as a waveguide for the cochlear traveling waves, the 3-D geometry in the basal cochlea is a poor waveguide. In the sound-port region of the cochlea, cochlear vibrations due to fast pressure transmission are non-negligible. As was seen in Temchin et al.'s (2012) measurement, the existence of the fast wave can confound the analysis of traveling wave onset delay. The implications of our results for the interpretation of otoacoustic emissions may warrant further investigation.

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COMMENTS AND DISCUSSION

[Jont Allen]: This is a very interesting argument you're making, and I partially agree with you, but I have an alternative explanation based on data. It shows this π phase-shift. You're seeing a π phase shift. Is that what it is? Seeing that in reversal in the phase. That's what you see in the phase. If so, you take the frequency derivative, you get the group delay.

[Jong-Hoon Nam]: Yes. Right.

[Jont Allen]: My paper was published in JASA. Its title is "A second cochlear-frequency map that correlates distortion products and neural tuning measurements". This π phase-shift was observed 'neurally' way back. It differs from what you're seeing in that if you do the experiment at a slightly different frequency, the π phase-shift moves with the CF. That's why I called it a

second cochlear frequency map. So, in some ways, it is a Greenwood (function) what you're saying. In other ways, it's just a partial explanation. I want to talk to you (later).

[Jong-Hoon]: Thank you for your input.

[Paul Kolston]: Lovely talk. I particularly liked your talk with animations. (As to) the first two animations you showed at the start, am I correct the lower one was showing the fast traveling wave?

[Jong-Hoon Nam]: (Indicating the impulse wave animation) No, there is no fast traveling wave here.

[Paul Kolston]: Ok. Thank you. I don't have a question then.

[Julien Meaud]: I like your simplified geometry modeling. But I am wondering what about, when you showed initially, the shaped of the duct is increasing in area toward the base. The round window is a part of it which is not like what you did in your model. Right? When you have a straight round window that is pretty long. How much do you think it would affect your results?

[Jong-Hoon Nam]: I do not know. However, the reason I stick to the rectangular shape is. If I make it 3-dimensional or cross-sectional area change, we are not sure if it is a sound port location effect or geometry changing effect. It becomes unclear. So intentionally we start from here to just see the sound port location effect. That's (3D geometry) is the next thing we can pursue.

[Sunil Puria]: Clearly the anatomy is always important. When you're modeling, especially finite element modeling when you want to figure out the layout. You show the possible importance of the round window being not at the end. In fact, I always remembered that in the cat the round window is in the middle of the cochlea practically. Right? So, I was wondered about that. I am glad you're looking at it. But then I was confused. In the active cochlea, it doesn't seem to matter, but in the passive cochlea it does matter. What's your guidance on that?

[Jong-Hoon Nam]: In active cochlea, as you might agree, outer hair cell action with (the help of) the Y-shaped structure probably favors the formulation of traveling waves so that it (traveling wave) overcomes the standing wave component. We need further study.